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A remarkable new species of small falcon from the Quaternary of Cuba (Aves: Falconidae: *Falco*)

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Abstract.—An enigmatic small falcon, *Falco kurochkini,* new species, is described from postcranial bones from several Quaternary sites in western and central Cuba. It was approximately intermediate in size between *F. sparverius* and *F. columbarius* but had proportionately longer and more slender leg elements than any living species of *Falco.* It is hypothesized that *F. kurochkini* may have been terrestrial, pursuing prey on foot, and that its extinction could have been related to terrestrial nesting habits as well.

Falcons of the genus *Falco* are poorly represented in the West Indies today. Two species, the Merlin (*F. columbarius*) and the Peregrine (*F. peregrinus*) are migrant or wintering birds from North America, although there are single breeding records of the latter from Cuba (Regalado & Cables 2000) and Dominica (Raffaele et al. 1998). Thus, the only truly resident *Falco* is the American Kestrel (*F. sparverius*), the smallest New World falcon, which is found throughout the Antilles. There are three endemic subspecies, of which by far the most distinctive is the Cuban *F. s. sparverioides,* which has three plumage phases—dark, light, and intermediate (Berovides & Fernández 1984), whereas the other taxa have no phases and are all more similar to the light phase of the Cuban bird. The Cuban subspecies has expanded relatively recently into the southern Bahamas and possibly to Jamaica and Hispaniola (Wotzkow 1998), although its occurrence on the last two islands does not appear to have been documented by specimens.

Considering this dearth of Antillean falcons, the discovery of a highly distinctive new fossil species in Cuba, also of small size, assumes considerable interest. We first learned of the existence of such a falcon in 1981, when E. N. Kurochkin showed one of us (SLO) a tarsometatarsus that he had collected in Camagüey eight years before. This specimen was so long and slender that it clearly could not be referred to any known species (Fig. 2E). Recently, Suárez was able to collect a considerable series of bones of this species representing most of the major postcranial elements, so that there is now sufficient material to characterize the new species.

Materials and Methods

Material examined.—Skeletons of the following species of Falconidae in the collections of the National Museum of Natural History, Smithsonian Institution (USNM): *Herpetotheres cachinnans, Caracara plancus, C. cheriway, Milvago chimango, M. chimachima, Daptrius americanus, D. ater, Phalcoboenus australis, Spiziapteryx circumcinctus, Polihierax insignis, Microhierax caerulescens, Falco mexicanus, F. rusticolus, F. peregrinus, F. rufigularis, F. biarmicus, F. cherrug, F. tinnunculus, F. vespertinus, F. rupicoloides, F. femoralis, F. cuvieri, F. eleonorae, F. subbuteo, F.*

cenchroides, F. longipennis, F. berigora. Measurements included in Table 1 were from *F. columbarius* USNM 18083, 291176, 291862, 291880, 300351, 322363, 429864, 499430, 499431–32, 554205, 560083, 610377–80, 610756; *Falco sparverius sparverioides* USNM 555159–69, 555175, 555524–25, 562459. Catalog numbers of fossil specimens formerly in the collection of William Suárez are indicated by WS.

Systematics

Class Aves
Family Falconidae

The new fossil species is referable to the Falconidae by the three distal openings in the tibiotarsus (the third may be only a deep pit in *Micrastur* and *Herpetotheres*), and by the longer and more centrally placed inner calcaneal ridge of the hypotarsus as opposed to the very short and medially placed ridge in the Accipitridae.

Genus *Falco* Linnaeus, 1758

The fossil agrees with *Falco, Polihierax,* and *Microhierax* in the absence of a procoracoid foramen in the coracoid, and in having the inner calcaneal ridge of the hypotarsus much longer, tapering gradually and extending over half the length of the shaft. In all other genera of Falconidae the procoracoid foramen is present and the inner calcaneal ridge of the hypotarsus is short and ends abruptly distally. These characters are also present in the small falcon *Pediohierax* Becker (1987) from the Miocene of North America. The species of *Polihierax* and *Microhierax* are the smallest members of the family, are entirely Old World in distribution, and are not obviously distinct from *Falco* osteologically. There is no reason to consider the Cuban fossil to be related to any of these smaller Old World taxa and it is therefore referred to the genus *Falco,* within which it is highly distinctive.

Falco kurochkini, new species
Figs. 1–2

Holotype.—Complete left tarsometatarsus, Museo Nacional de Historia Natural de Cuba MNHNCu P3229, formerly WS 1054. Collected 4 May 1997 by William Suárez.

Type locality.—Cuba, La Habana province, municipality of Caimito, Llanura Meridional Habanera, about 4 km south of the town of Vereda Nueva, "Cueva de Sandoval," in a small sink within the cave known as "El Sumidero" (see Suárez 2000).

Chronology.—Quaternary, probably Pleistocene but not directly dated.

Measurements (mm) of holotype.—See Table 1.

Paratypes.—The following are topotypes. Right coracoid MNHNCu P3209 (WS 1071); left coracoid USNM 510237 (WS 1070). Humerus: complete left MNHNCu P3210 (WS 1068), USNM 510238 (WS 1046), left lacking pectoral crest USNM 510239 (WS 1055), incomplete left MNHNCu P3211 (WS 0195), proximal lefts MNHNCu P3212, P3213, P3214 (WS 1056, 1057, 1069), right lacking proximal end MNHNCu P3215 (WS 1049), proximal right USNM 510238 (WS 1058), distal right USNM 510241 (WS 1078). Ulna: proximal right MNHNCu P3217 (WS 1065), USNM 510242 (WS 1063); distal right MNHNCu P3219 (WS 1072); proximal left MNHNCu P3216 (WS 1064); distal left MNHNCu P3218 (WS 1073), USNM 510249 (WS 1074). Carpometacarpus: proximal right MNHNCu P3220 (WS 1045). Notarium: MNHNCu P3221 (WS 1080). Femur: complete left MNHNCu P3222 (WS 1048), USNM 510243 (WS 1067); distal half of right MNHNCu P3226 (WS 0198); left lacking distal end MNHNCu P3223 (WS 0196); proximal left MNHNCu P3224 (WS 1077), MNHNCu P3225 (WS 1047), USNM 510244 (WS 1061). Tibiotarsus: complete right MNHNCu P3227 (WS 1066); complete left USNM 510245 (WS 1053); proximal half of left USNM 510246 (WS 1043);

Table 1.—Measurements (mm) of skeletal elements of small species of Cuban *Falco*. Sequence is: range (mean) n.

Measurement	*F. kurochkini*, n. sp.	*F. sparverius sparverioides*	*F. columbarius*
NOTARIUM			
Length	20.9	14.5–19.1 (18.2) 14	24.1–27.7 (26.2) 16
CORACOID			
Head to internal distal angle	27.3	21.6–23.2 (22.3) 15	27.0–31.5 (29.2) 17
Procoracoid to internal distal angle	19.0–20.6 (19.8) 2	15.9–17.2 (16.5) 15	19.6–23.5 (21.6) 17
HUMERUS			
Length	45.8–49.4 (47.7) 3	39.5–43.1 (41.1) 14	43.7–51.0 (48.1) 16
Proximal width from internal to external tuberosities	8.7–9.8 (9.2) 7	7.8–8.8 (8.4) 15	9.3–12.5 (11.0) 16
Shaft width at midpoint	3.6–4.2 (4.0) 7	2.3–2.6 (2.5) 15	4.1–4.8 (4.4) 16
Distal width	7.4–8.4 (7.9) 5	7.0–7.4 (7.2) 15	8.5–10.2 (8.8) 16
ULNA			
Proximal width	4.0–4.5 (4.2) 3	3.8–4.1 (3.6) 15	4.7–6.1 (5.1) 16
Width of shaft at midpoint	2.8–3.2 (3.0) 5	2.3–2.6 (2.5) 15	4.1–4.8 (4.4) 16
Distal width	5.1–5.2 (5.1) 3	4.5–5.1 (4.8) 15	5.1–6.7 (6.0) 15
CARPOMETACARPUS			
Proximal width	3.1	2.9–3.4 (3.1) 15	3.3–4.1 (3.7) 17
Proximal depth	7.0	6.4–7.2 (6.8) 15	8.0–9.5 (8.6) 17
FEMUR			
Length	45.7–48.2 (46.9) 2	34.5–37.2 (35.9) 15	41.1–47.2 (44.3) 17
Proximal width	6.6–7.3 (7.1) 5	5.5–6.2 (5.9) 15	6.8–8.2 (7.3) 18
Shaft width at midpoint	3.5–3.9 (3.7) 5	2.7–3.2 (2.9) 15	3.4–4.3 (3.7) 18
Distal width	6.7–7.4 (7.2) 3	4.5–5.1 (4.8) 15	6.8–8.0 (7.3) 18
TIBIOTARSUS			
Length	60.8–68.9 (64.4) 2	47.6–51.8 (49.9) 11	52.3–60.7 (56.8) 17
Proximal width	6.5	4.7–5.6 (5.1) 14	5.6–7.1 (6.3) 17
Length of fibular crest	9.5–10.7 (10.0) 4	6.4–8.3 (7.6) 14	6.9–9.3 (8.2) 17
Shaft width at midpoint	3.0–3.4 (3.3) 4	2.3–2.9 (2.6) 13	2.6–3.3 (2.9) 17
Distal width	5.5–6.3 (6.0) 3	5.0–5.6 (5.3) 14	5.9–7.0 (6.5) 17
TARSOMETATARSUS			
Length	49.6*	34.5–37.3 (36.0) 15	34.6–39.9 (37.2) 17
Proximal width	6.6*	5.2–5.7 (5.5) 15	6.1–7.4 (6.7) 17
Shaft width at midpoint	3.0–3.1* (3.1) 3	2.1–2.6 (2.3) 15	2.2–2.9 (2.6) 17
Distal width	5.9–6.7* (6.3) 2	5.2–6.1 (5.7) 15	5.9–7.3 (6.7) 17

* Holotype.

distal right MNHNCu P3228 (WS 1062). Tarsometatarsus: right, lacking proximal end USNM 510247 (WS 1059); shaft of left USNM 510248 (WS 1060).

Cuba, La Habana province, municipality of Caimito, ca. 3 km SE of Ceiba del Agua, "Cueva de Paredones" (see Arredondo 1971, 1976), in a sink known as "Salón del Pozo," collected 5 March 1994 by William Suárez: right tibiotarsus lacking proximal end MNHNCu 3230 (WS 1081).

Cuba, Camagüey province, 28.5 km NE of Camagüey, "Cueva de los Fósiles" (see Olson 1985, Olson & Kurochkin 1987), collected in 1973 by E. N. Kurochkin: left tarsometatarsus lacking distal end (Fig 2E) Instituto de Geología y Paleontología, Habana, Cuba, 406-3.

Measurements (mm) of paratypes.—See Table 1.

Etymology.—Dedicated to our colleague and friend Evgeny N. Kurochkin, of the Paleontological Institute of the Russian Academy of Sciences, for his many contributions to avian paleontology and in recognition of his paleontological explorations in Cuba during which he found the first known specimen of the new species described here.

Diagnosis.—A small species of *Falco,* larger than *F. sparverius sparverioides* and with some measurements within the size range of *F. columbarius* but hindlimb elements proportionately much longer and more slender than in any known species of *Falco.*

Description.—Coracoid with shaft more slender, sternal facet in dorsal view narrower, deeper, and more rounded than in *F. columbarius* or *F. sparverius.* Humerus with shaft more slender, elongate, and sigmoid, resulting in a proportionately greater distance between the distal extent of pectoral crest and the distal extremity. Pectoral crest and entepicondylar process not as expanded as in *F. columbarius.* Lack of complete specimens of the ulna and carpometacarpus prevent adequate comparisons, except to note that the shaft is more robust in the new species than in *F. sparverius.*

Notarium more slender and slightly larger than in *F. sparverius.* Femur with very long slender shaft, head more constricted at base and more distinctly set off from the neck, depression for ligamentum teres less distinct, distal end of femur relatively narrower. Tibiotarsus with shaft extremely slender, proximal and distal ends relatively narrower, fibular crest longer, distal point of fusion of fibula much higher on the shaft, most proximal tendinal opening of distal end higher on the shaft. Tarsometatarsus also extremely long and slender, proximal end of inner calcaneal ridge of hypotarsus situated lower on shaft relative to proximal articular surface, distal portion of shaft relatively wider so that trochleae appear less flared, wing of inner trochlea less distinct and pointed.

Substantial size variation between some of the elements (e.g., tibiotarsi USNM 510245 and MNHNCu 3230) are strongly suggestive of sexual dimorphism in size, with presumed males being smaller as in many species of raptors.

Remarks.—There are no obvious clues to the derivation of *F. kurochkini* within the genus *Falco,* as no other species has such an elongate, slender hindlimb. The Australian Brown Falcon *F. berigora* has the most elongated tarsometatarsus of any living species of the genus, but this is a much larger bird in which the other elements of the hindlimb are not as slender proportionately as in *F. kurochkini.* The general similarity of the fossil species is closer to that of *F. sparverius* than to the stronger and more robust *F. columbarius,* but this similarity could be the result of both being smaller, weaker birds.

The singular nature of *F. kurochkini* naturally raises obvious questions concerning its habits, ecology, and extinction. It is unlikely that climatic fluctuations in the Quaternary or overhunting by paleoindians would cause the disappearance of a small, volant predatory bird, particularly considering that *Falco sparverius* still thrives and is abundant in Cuba (Garrido & García Montaña 1975).

Falco sparverius had previously been reported in Cuba in a Quaternary cave deposit in Habana Province (Jiménez Vázquez 1997). It occurs in association with *F. kurochkini* at the type locality (Suárez 2000) and at Paredones Cave as well (Suárez, pers. obs.), where its remains probably accumulated as prey items of the extinct barn owl *Tyto noeli.* Thus, these two small falcons co-existed in both time and space and presumably either exploited different food sources, or obtained similar prey species in a different manner.

How did *F. kurochkini* hunt and what was its prey? In some raptors (Accipitridae, Strigidae), elongation of the hindlimb, particularly the tarsometatarsus, is thought to

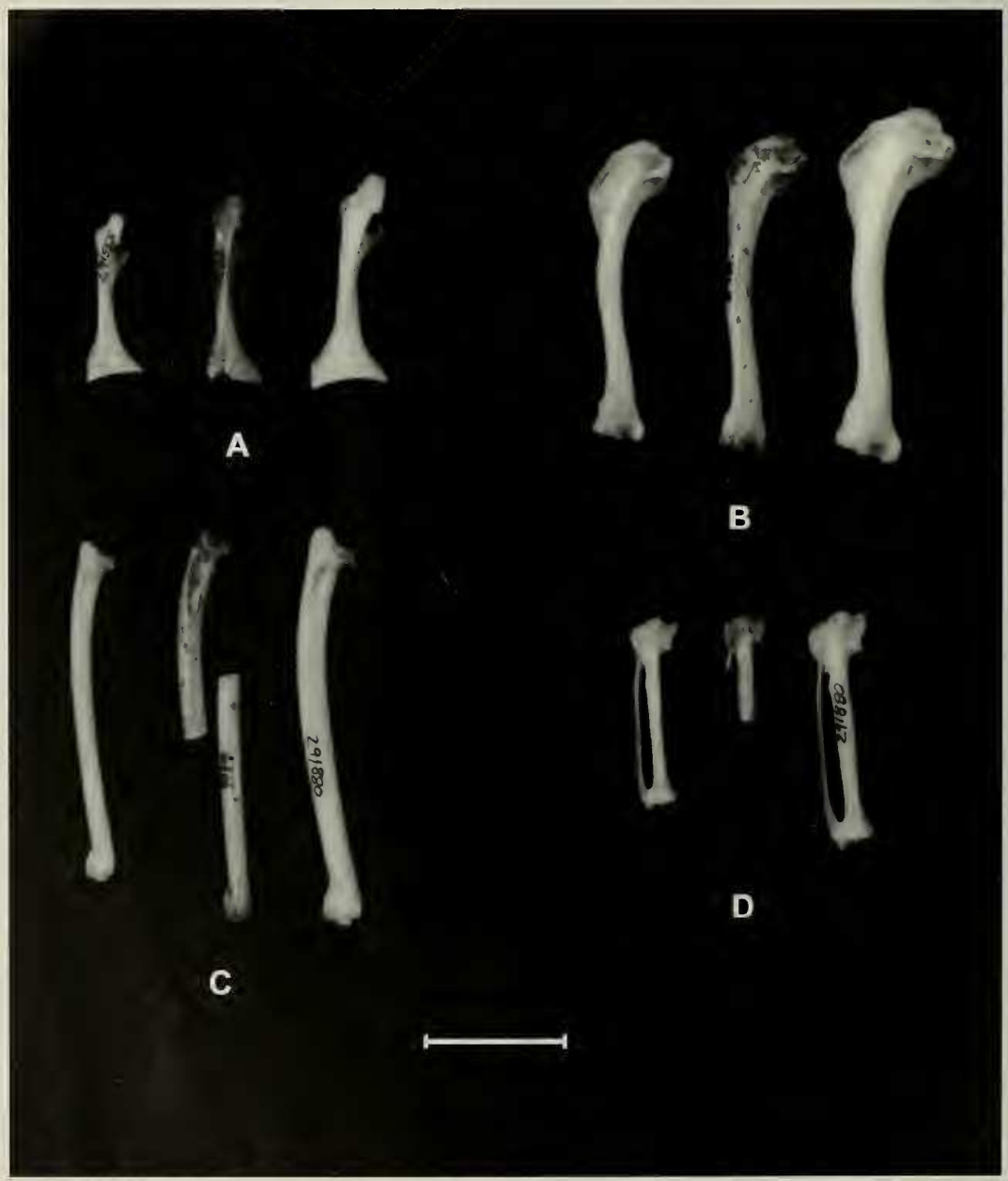

Fig. 1. Pectoral elements of *Falco kurochkini*, new species (middle bone in each group), compared with *F. sparverius sparverioides* USNM 555167 (left in each group) and *F. columbarius* USNM 291880 (right in each group): A, right coracoids in ventral view (paratype MNHNCu P3209); B, left humeri in anconal view (paratype MNHNCu 3210); C, left ulnae in internal view (paratypes MNHNCu 3216 and USNM 510249); D, right carpometacarpi in external view (paratype MNHNCu P3220). Scale = 2 cm.

be associated with preying on birds (Olson & James 1991), but *F. columbarius* feeds almost exclusively on birds and has no such adaptation. *Falco sparverius* is primarily insectivorous; *F. kurochkini* was not much larger and quite likely also fed on insects, and perhaps on lizards. Why then, does it have such remarkable leg proportions?

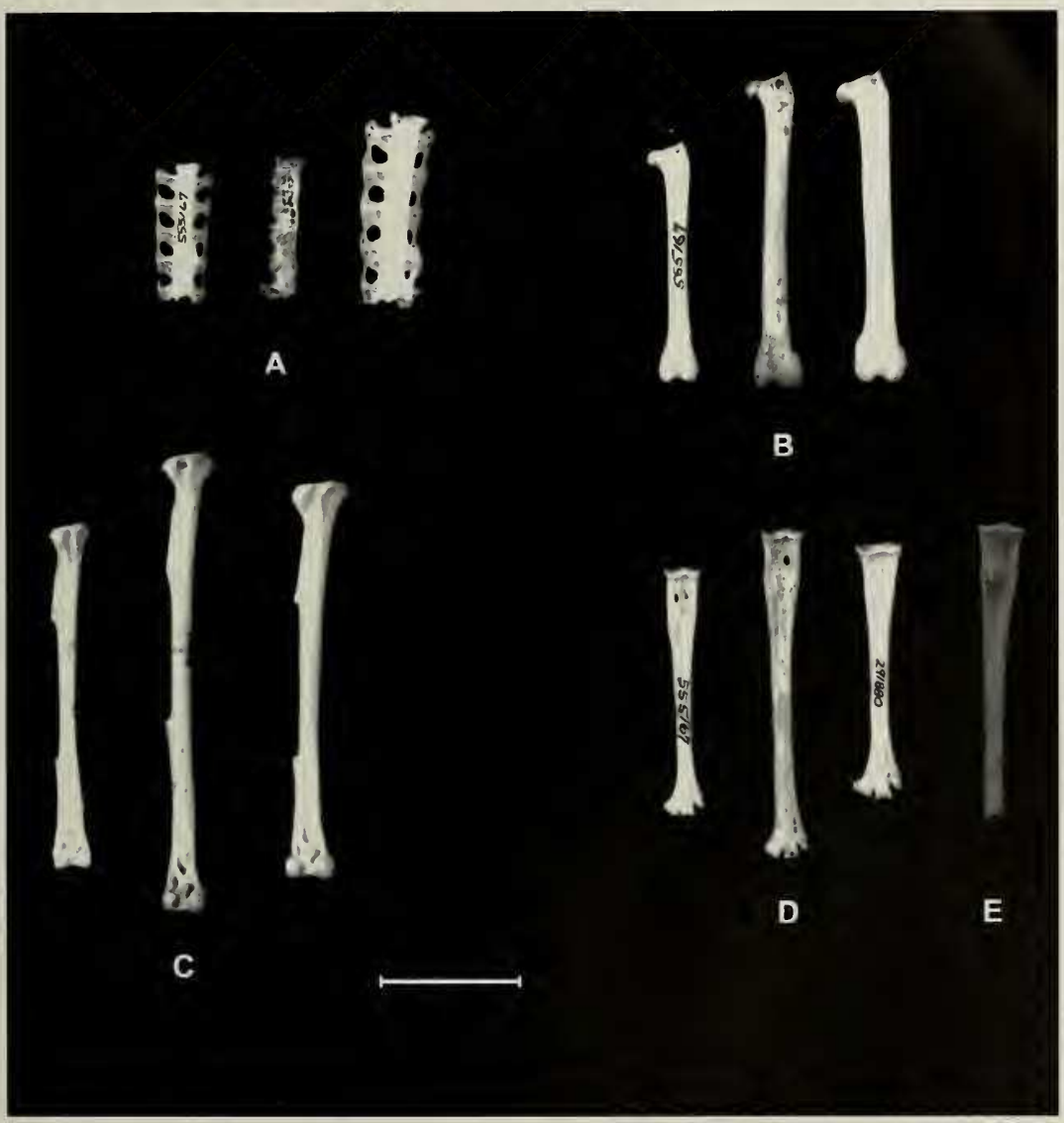

Fig. 2. Notarium and hindlimb elements of *Falco kurochkini,* new species (middle bone in each group), compared with *F. sparverius sparverioides* USNM 555167 (left in each group) and *F. columbarius* USNM 291880 (right in each group): A, notaria in ventral view (paratype MNHNCu P3221); B, left femora in anterior view (paratype MNHNCu P3222); C, right tibiotarsi in anterior view (paratype MNHNCu 3227); D, tarsometatarsi in external view (holotype MNHNCu P3229); E, left tarsometatarsus lacking distal end from Camagüey (paratype Instituto de Geología y Paleontología 406-3). Scale = 2 cm.

The habits of the long-legged Australian *Falco berigora* may provide a clue to the adaptations of *F. kurochkini.* The former is an opportunistic carnivore and scavenger that may feed upon prey from the size of rabbits to insects (Marchant & Higgins 1993). It uses various methods of hunting including soaring, low quartering, or sallying from a perch. More interestingly, however, it also hunts on the ground, where it may run after prey (Fig. 3), which is quite unlike other species of *Falco.* We suggest, therefore, that *F. kurochkini* may have been a terrestrial bird of open country, stalking

Fig. 3. Stances of the Australian Brown Falcon *Falco berigora* when feeding on the ground. It is hypothesized that perhaps the adaptations of the extinct Cuban fossil *Falco kurochkini* new species, may have been for a more terrestrial existence than in other species of the genus. (Figure from Marchant & Higgins, 1993, p. 240).

prey such as insects and lizards on the ground. It could then be viewed as occupying the niche of a diminutive caracara (e.g., *Caracara, Milvago*), the caracaras being more terrestrially adapted members of the Falconidae.

Species of *Falco* do not usually build their own nests. *Falco sparverius* nests in cavities, usually in trees, but most other species appropriate the disused nests of other raptors, or nest on ledges, hollows in rocks, or even on the ground. In Australia, *F. berigora* usually uses old nests of other raptors but may lay its eggs in a depression in the "ground, ledges, or in holes" (Marchant & Higgins 1993: 247). The New Zealand Falcon *F. novaeseelandiae,* which evolved on islands with no native terrestrial predators, places its nest "on ledges of cliffs . . . on ground on steep broken hillsides, easily accessible, at foot of rocky overhang and usually screened by vegetation . . . on ground under log without much screening vegetation . . . in epiphytes on trees" (Marchant & Higgins 1993: 287).

In Cuba, where the only native mammalian predators were two genera of Insectivora, *Falco kurochkini* likewise may have nested on the ground or in holes or crevices in embankments or hillsides. Such nesting habits may have made it more vulnerable to increased burning after the arrival of Amerindians and to destruction by introduced mammals such as rats (*Rattus*) following European colonization in the 16th century.

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